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Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*)

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Summary

1. In birds with bi-parental care, handicapping is often assumed to decrease the amount of parental care of the handicapped partner. We discuss how handicapping could alter the shape of the handicapped bird's survival–effort curve (theoretical curve relating the survival of a parent to its effort) and show that the optimal response could yield a decrease, no response or even an increase in effort of the handicapped bird.

2. Male or female great tits *Parus major* (L.) were handicapped during the nestling period by clipping a number of feathers in order to study the effects on parental care and body condition.

3. Handicapped males significantly decreased their feeding rates, while handicapped females did not. Condition of handicapped females significantly deteriorated, while condition of handicapped males did not change during the experiment. Females with a handicapped partner fully compensated for their partner's decrease in work rate, while males with a handicapped partner did not show any compensation and even tended to decrease their feeding rates.

4. Using an inverse optimality approach, we reconstructed the theoretical curve relating the survival of a parent to its effort on the basis of the experimental effects. The handicapped male's survival–effort curve appeared to be slightly steeper than that of handicapped females. This suggests that handicapped males suffer more from an increase in effort than handicapped females.

Key-words: bi-parental care, great tit, handicapping manipulation, parental effort, *Parus major*.

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Introduction

In situations of bi-parental care a conflict of interests may arise owing to differences in the optimal level of investment in the brood for each partner (Trivers 1972). The solution to this conflict determines the equilibrium for co-operation between the parents (Smith *et al.* 1988), and has been modelled as an evolutionary stable strategy (Chase 1980;

Houston & Davies 1985) and as an optimal investment strategy (Winkler 1987; Kacelnik & Cuthill 1990). While the level of investment by each partner may be influenced by many factors, such as parent–offspring relatedness, age and number of young, or condition of parent and offspring, we limit ourselves in the present study to the response of a parent to its partner's contribution and to being handicapped itself.

In bi-parental bird species, researchers have handicapped one parent, by either clipping a number of feathers (Verbeek & Morgan 1980; Slagsvold & Lifjeld 1988; Slagsvold & Lifjeld 1990; Whittingham, Dunn & Robertson 1994; Weimerskirch, Chastel & Ackermann 1995) or by attaching weights to the birds (Wright & Cuthill 1989; Wright & Cuthill 1990a,b; Sæther, Andersen

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& Pedersen 1993; Markman, Yom-tov & Wright 1995), to investigate the response of one parent to a reduction in parental investment of its partner. These experimental studies show a range of responses to a reduction in a partner's parental care, from no response through incomplete compensation to complete compensation. Evolutionary stable strategy models suggest that bi-parental care will be stable when parents partially compensate for changes in care by the other parent (Chase 1980; Houston & Davies 1985). The shape of the theoretical curve relating the survival of a parent to its effort (concave-down vs. convex-down) affects the likelihood that the parent will compensate reduced care by the other partner (Ratnieks 1996). The stability of bi-parental care in birds may be caused by a concave down curve for future parental fitness vs. total effort put into chick rearing by that parent (Ratnieks 1996). Moreover, a deteriorating body condition in the handicapped parent has also been found (Slagsvold & Lifjeld 1988; Slagsvold & Lifjeld 1990; Weimerskirch *et al.* 1995). Depending on the particular effect of handicapping, both diminishing parental care and deteriorating body condition might be expected as an optimal response to being handicapped.

Following Houston & Davies (1985) we simplified our fitness measure to the number of young that survive to breed, plus the parent's probability of surviving to the next season. Also, we assume that each parent treats all members of the brood equally (Houston & Davies 1985; Kölliker *et al.* 1998). The survival of a nestling is assumed to increase at a decreasing rate as parental effort increases (nestling survival curve, Fig. 1a), while the survival of a parent is assumed to decrease at an increasing rate as effort increases (parental survival-effort curve, line a, Fig. 1b). Convenient equations to represent this are:

$$\text{Nestling survival} = 1 - e^{-(E_i + E_o)} \quad \text{eqn 1}$$

$$\text{Parent's survival} = f - f \cdot e^{-1+c \cdot E_i} \quad \text{eqn 2}$$

where E_i is the effort that individual i devotes to each nestling (note that individual's total effort is required to lie between 0 and 1), E_o is the effort of its partner, c and f are parameters that might alter the survival-effort curve. Parental effort as used here is the absolute amount of effort delivered to the brood, not the proportion of resources committed to parental effort (Winkler 1987). A concave-down parental survival-effort curve as line a in Fig. 1(b) means that each increment of effort is more costly to the parent than the previous increment (Ratnieks 1996).

One single parental survival-effort curve is assumed to be applicable to both members of a pair (Houston & Davies 1985). In the present study, parameters f and c are manipulated to mimic different potential effects of handicapping on the parental survival-effort curve of the handicapped birds (note that all the other parameters, as brood size or food availability, that might alter this curve are kept constant). The parental survival-effort curve of its non-handicapped partner is assumed to remain constant. Handicapping is assumed not to influence the shape of the nestling survival curve. The types of effects of handicapping on the survival-effort curve of the handicapped parent we propose here are as follows.

1. Survival decreases at an increasing rate, compared to the non-handicap situation, as effort (measured as provisioning rate) increases, which implies that the fitness costs of handicapping are positively related to effort. In the simplest case this can be imagined when handicapping affects the foraging efficiency negatively. This effect can mathematically be achieved by an increase in parameter c (line b, Fig. 1b).

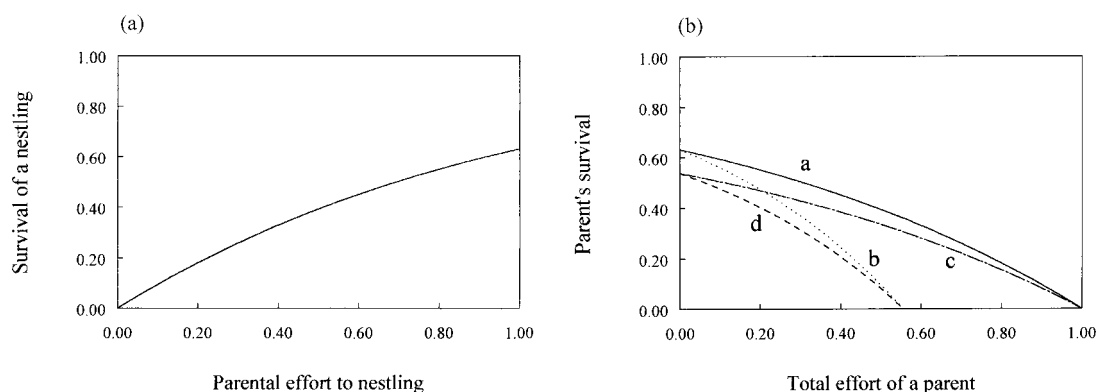


Fig. 1. Theoretical curves of: (a) nestling survival as a function of total parental effort; (b) of survival of a parent as a function of its effort in a control situation (line a), in a handicap situation with either a type 1 effect (line b), a type 2 effect (line c) or a type 3 effect (line d).

2. Survival decreases at a decreasing rate, compared to the non-handicap situation, as provisioning rate increases, which implies that handicapping decreases survival independently of effort. One way to imagine such an effect is that handicapping reduces the probability to escape a predator and that, in addition, the chance of a predator attack is independent of effort. Such an effect would be most likely when predation on handicapped birds would occur after independence of the offspring. This effect can mathematically be achieved by a decrease in parameter f (line c , Fig. 1b).

3. A mixture of the two effects. This effect can mathematically be achieved by both an increase in parameter c and a decrease in parameter f (line d , Fig. 1b).

The optimal effort of individual i as a function of the effort of other parent (o) can be found by choosing E_i so as to maximize:

$$1 - e^{-(E_i + E_o)} + f - f \cdot e^{-1 + c \cdot E_i} \quad \text{eqn 3}$$

The maximum can be found by differentiating equation 3 with respect to E_i and setting the result equal to 0. Following this procedure, we find that the optimal effort, E_i^* , is given by the equation:

$$E_i^* = \frac{1 - E_o \ln fc}{1 + c} \quad \text{eqn 4}$$

Assuming that individual i is the handicapped bird and individual o the non-handicapped partner, the survival effort curve of the non-handicapped bird (o) will not be changed, allowing parameters c and f to remain constant at an assumed default level of 1. Thus, the optimal effort of the non-handicapped partner, E_o^* , is given by the equation:

$$E_o^* = \frac{1 - E_i}{2} \quad \text{eqn 5}$$

If we allow both parents to adopt their optimal level of investment (E_i^o , E_o^o), both equations 4 and 5 have to be met. By elimination of E_o from equation 4 using equation 5, we yield:

$$E_i^o = \frac{1 - 2 \cdot \ln fc}{1 + 2 \cdot c} \quad \text{eqn 6}$$

and similarly

$$E_o^o = \frac{c + \ln fc}{1 + 2 \cdot c} \quad \text{eqn 7}$$

These equations can be used to express the optimal effort of a handicapped bird and its non-handicapped partner as a function of parameters c and f . Equations 6 and 7 can also be used to express nestling survival (equation 1) and parental survival (equation 2) of both handicapped and non-handicapped birds, as a function of parameters c and f . The following patterns emerge:

1. A type 1 effect (an increase of parameter c) is expected to evoke a decrease in the effort of a handicapped parent, which will press its partner to increase its effort (note that this compensatory response is expected to be incomplete; Chase 1980; Houston & Davies 1985). Nestlings are expected to survive less well because of the incomplete compensatory response of the non-handicapped parent. Moreover, this type 1 effect yields increased survival probabilities in the handicapped parent and a slight decreased survival probabilities in the non-handicapped partner.

2. A type 2 effect (a decrease of parameter f) is expected to evoke an increase in the effort of a handicapped parent and a decrease in the optimal effort of the non-handicapped partner. This will result in a slight increase in nestling survival, a decrease in survival of the handicapped parent and a slight increase in survival of the non-handicapped partner.

3. A combination of changes in c and f (a type 3 effect) may yield quite a range of effort and survival combinations. However, there is one class of c - f combinations that results in the same optimal effort for both parents and the same nestling survival as in the non-handicap situation. Mathematically, this class of c - f combinations can be expressed as:

$$f = \frac{e^{1/3}}{c \cdot e^{c/3}} \quad \text{eqn 8}$$

This class of c - f combinations defined by equation 8 results in a decreased survival of the handicapped parent, which is now the only effect of handicapping.

In the present study we directly investigated the response of male and female great tits *Parus major* to an experimental reduction in the partner's feeding contribution. In the great tit, male and female participated equally in the feeding of nestlings (Smith *et al.* 1988). Adults were handicapped by clipping a number of feathers (Slagsvold & Lifjeld 1990) and the effects were monitored both in terms of parental care during the nestling period (measured as feeding rates and faeces removal rates) and body condition of parents as well as of offspring. In this way it might be possible to assess the type of effect this handicapping has on the survival-effort curve.

Methods

GENERAL METHODS

The study was conducted in a mixed deciduous forest in the Lauwersmeer area (The Netherlands, 53°20' N, 06°12' E). In 1996, nestboxes were checked for occupation by great tits, and laying date and clutch size were recorded. Nests were checked daily around the expected day of hatching to establish the hatching date. Adults were captured with spring traps when the young were 9- and 15-day-old

(day of hatching = 0), ringed, weighed and their tarsus was measured. Nestlings were weighed and measured when they were 14-day-old. All birds were weighed to the nearest 0.1 g with a spring balance and their tarsus length was measured to the nearest 0.1 mm with a dial caliper.

EXPERIMENTAL PROCEDURES

While rearing their first brood, 90 great tit pairs were randomly assigned to either a group in which the female was going to be handicapped ($n = 30$ pairs), a group in which the male was going to be handicapped ($n = 27$ pairs) or the control group in which neither of the two parents was going to be handicapped ($n = 33$ pairs). There is only a slight degree of dimorphism in size in the great tit, suggesting that the cost of feeding nestlings is similar for both sexes (Smith *et al.* 1988). There were no differences in laying date (ANOVA, $F_{2,87} = 2.01$, $P = 0.14$), clutch size ($F_{2,87} = 1.63$, $P = 0.20$), hatching date ($F_{2,87} = 0.14$, $P = 0.87$) or brood size on day 8 after hatching ($F_{2,87} = 0.001$, $P = 0.99$) among experimental groups. In the three experimental groups, feeding rates and faeces removal rates by both parents were recorded on days 8 and 12 after hatching of their broods (13 control, 14 female handicapped and 13 male handicapped pairs). Nestboxes were monitored for 3 h using a video camera. These data were averaged to periods of 1 hour. Ambient temperature was recorded during video monitoring by a TINYTALK™ data logger. After video recording on day 8 after hatching, brood mass was determined. Feeding rates on both days 8 and 12 after hatching of their brood showed no significant trend with time of the day and ambient temperature (ANCOVA, day 8: time of day: $\beta = 0.60$, $t_{72} = 1.04$, $P = 0.30$; ambient temperature: $\beta = -0.17$, $t_{72} = 0.56$, $P = 0.58$. Day 12: time of day: $\beta = -0.07$, $t_{70} = 0.17$, $P = 0.86$; ambient temperature: $\beta = -0.52$, $t_{70} = 1.86$, $P = 0.07$). On day 12 after hatching, there was no two-way interaction effect between experimental group and time of the day ($F_{2,70} = 1.05$, $P = 0.36$). We have used all behavioural variables without correction for time of the day or ambient temperature.

On day 9 after hatching, adult birds were captured in their own nestboxes using a spring trap. After the measurements, the birds were handicapped or not according to the group they were previously assigned to (licence BG19396). Handicapping involved clipping of the primaries, numbers 5, 7 and 9, counted from the outside, on each wing, together with the six central tail feathers (Slagsvold & Lifjeld 1990). The feather was cut near its base. The effect of this treatment was only temporary since feathers are replaced during the post-breeding moult. There neither seem to be long-term adverse effects, with at

least 17.5% of the handicapped birds (18% for control pairs) going on to start second broods after the successful fledgling of their first broods. On day 15 after hatching, parents were captured and weighed again. The total mass of the removed feathers was on average 0.1 g. Therefore, body masses of handicapped birds on day 15 after hatching were corrected for this artificial mass loss by adding 0.1 g to their body mass.

Female and male body mass on days 9 and 15 after hatching of their brood did not show any trend with capture time (female: day 9: $r_{89} = 0.11$, $P = 0.30$; day 15: $r_{80} = -0.03$, $P = 0.78$; male: day 9: $r_{81} = -0.001$, $P = 0.99$; day 15: $r_{70} = 0.09$, $P = 0.47$). Therefore, we have used body mass data uncorrected for capture time. Neither did adults differ in tarsus length among experimental groups (females: $F_{2,87} = 2.71$, $P = 0.072$; males: $F_{2,82} = 0.05$, $P = 0.95$). Handicapped females had longer tarsus length than those with a handicapped partner (LSD *a posteriori* test, $P = 0.02$). Moreover, adult body mass on day 9 after hatching was positively correlated with their tarsus length (females: $r_{89} = 0.51$, $P < 0.001$; males: $r_{81} = 0.44$, $P < 0.001$). We have therefore used repeated-measures ANCOVAs with experimental treatment, and parental sex as factors and tarsus length as covariate.

STATISTICAL PROCEDURES

Each nest was assumed to be a statistically independent observation, and mean body mass and tarsus length of the offspring was used in the analyses. Feeding rates on days 8 and 12 after hatching did not differ from a normal distribution (Kolmogorov–Smirnov test, all $P > 0.30$). Percentages (fledging success) were analysed after arc-sine square root transformation. In presenting the results of repeated-measures ANOVAs or ANCOVAs, where particular between-group comparisons were of interest the least significant difference (LSD) *a posteriori* test (which take into account the number of comparisons) are given, in addition to the overall F ratios (SPSS Inc. 1988). Means are presented with SD.

Results

PARENTAL EFFORT

Male, female and total feeding rates per hour for each experimental group for the two brood ages (days 8 and 12 after hatching) are shown in Fig. 2. The results of a repeated-measures ANOVA by experimental treatment, parental sex and brood age are presented in Table 1. There was a significant two-way interaction term between parental sex and brood age owing to a significant decrease in male feeding rates on day 12 relative to day 8 (LSD *a posteriori* test, $P = 0.006$), and a non-significant dif-

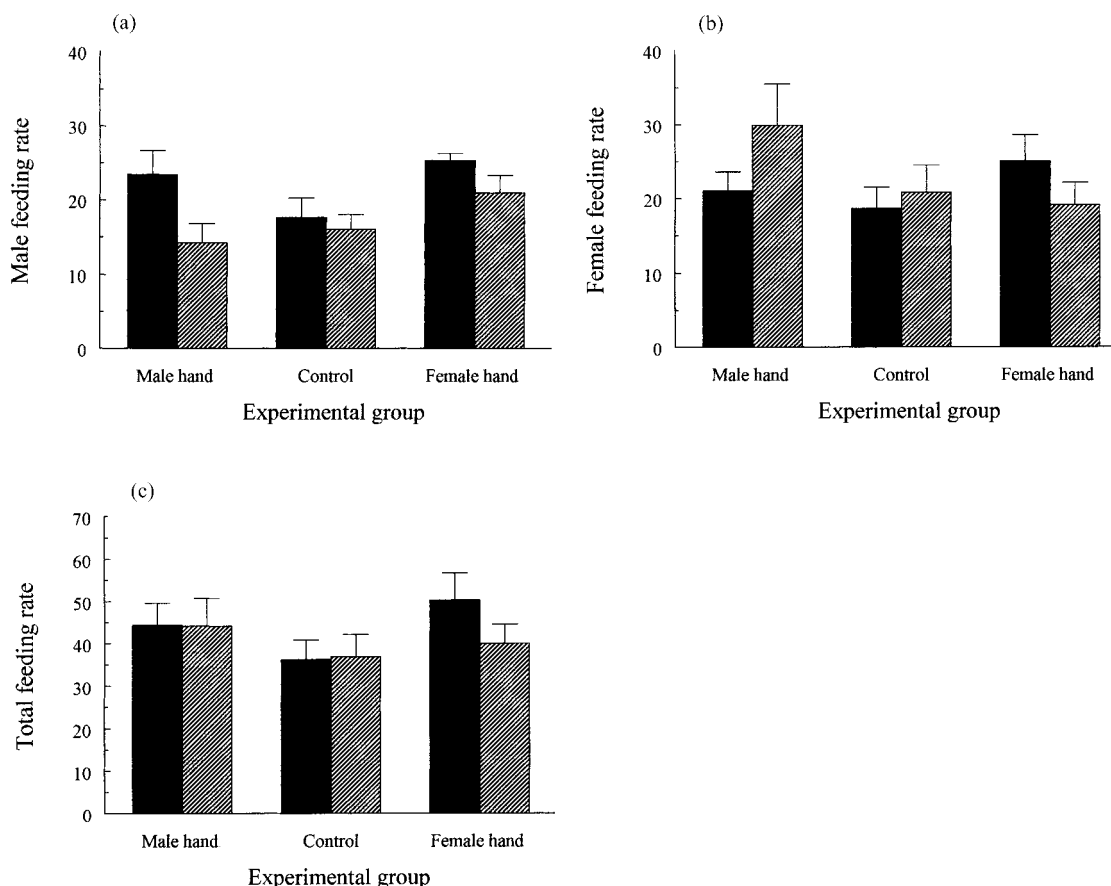


Fig. 2. Mean feeding rates of (a) males, (b) females and total provisioning rate (c) in the three different treatments groups (solid bars, feeding rates before handicapping; diagonally lined bars, feeding rates after handicapping). The error bars represent the standard error of the mean.

ference in female feeding rates between days 8 and 12 (LSD *a posteriori* test, $P = 0.34$). There was a significant three-way interaction term among experimental group, parental sex and brood age (Table 1). This can be explained because handicapped males reduced their feeding visits from days 8–12 (LSD *a posteriori* test, $P = 0.005$; Fig. 2a) and their females increased their feeding visits from days 8–12 (LSD *a posteriori* test, $P = 0.006$; Fig. 2b). In the control group, male and female feeding rates did not differ between days 8 and 12 after hatching (LSD *a posteriori* tests, $P = 0.61$ and $P = 0.49$, respectively). In the female handicapped group, female feeding rates did not differ between days 8 and 12 (LSD *a posteriori* test, $P = 0.15$), and males did not change feeding rates between those days, although the effect was close to significant (LSD *a posteriori* test, $P = 0.056$; Fig. 2a). Mean feeding rates on day 8 after hatching of their brood did not differ between sexes in the three experimental groups (LSD *a posteriori* tests; control, $P = 0.75$; male handicap, $P = 0.45$; female handicap, $P = 0.92$). This suggests that changes in either of the handicapped groups

can be fully ascribed to the experimental manipulation. Mean feeding rates on day 12 after hatching did not differ between sexes in both control and female handicapped groups (LSD *a posteriori* tests,

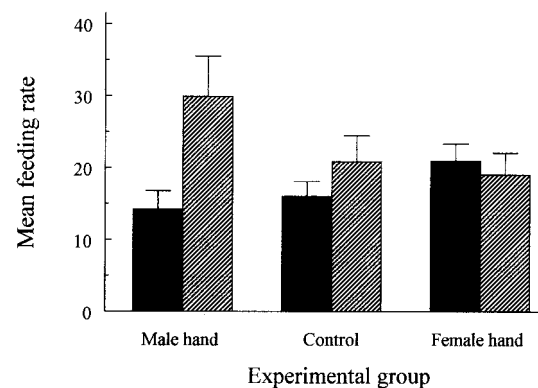


Fig. 3. Mean (+ SE) nest visits rates per hour on day 12 after hatching, according to experimental group and sex (solid bars, males; diagonally lined bars, females).

Table 1. The results of repeated-measures ANOVA and ANCOVA on mean parental feeding rates per hour and mean parental faeces removal rate per hour. The effects of experimental group (Group), parental sex (Sex) and brood age (Age), and all interaction terms are shown as *F*-ratios, degrees of freedom (d.f.) and their *P*-values

		<i>F</i>	d.f.	<i>P</i>
Feeding rate	Factor			
	Group	1.33	2,74	0.27
	Sex	1.44	1,74	0.23
	Age	1.71	1,74	0.20
	Group × Sex	0.91	2,74	0.41
	Group × Age	1.93	2,74	0.15
	Sex × Age	7.17	1,74	0.009
	Group × Sex × Age	5.31	2,74	0.007
Faeces removal rate	Changing covariates			
	Feeding rates on day 8	11.16	2,72	< 0.001
	Feeding rates on day 12	17.49	2,72	< 0.001
	Factor			
	Group	2.02	1,73	0.14
	Sex	1.65	1,73	0.20
	Age	0.05	1,73	0.83
	Group × Sex	0.34	2,73	0.72
	Group × Age	1.06	2,73	0.35
	Sex × Age	6.74	1,73	0.011
	Group × Sex × Age	1.75	2,73	0.18

$P = 0.13$ and $P = 0.55$, respectively), while in the male handicapped group, feeding rates on day 12 did differ significantly between sexes, with lower values for males (LSD a posteriori test, $P < 0.001$; Fig. 3).

Total feeding visits per nest showed no significant differences among the experimental groups (repeated-measures ANOVA; $F_{2,37} = 0.84$, $P = 0.44$; Fig. 2c), and did not differ between days 8 and 12 after hatching ($F_{1,37} = 2.10$, $P = 0.16$). Moreover, there was no significant experimental group by brood age interaction effect ($F_{2,37} = 2.37$, $P = 0.11$).

Faeces removal rate of both parents was positively correlated with their number of feeding visits to the nest (females: $r_{79} = 0.60$, $P < 0.001$; males: $r_{79} = 0.46$, $P < 0.001$). As faeces removal rate depends on feeding rate, a repeated-measures ANCOVA was performed with experimental group, parental sex and brood age as factors, and feeding

rates on days 8 and 12 as changing covariates (Table 1). When the effect of feeding visits was controlled for, there were no significant differences between sexes and among experimental groups in terms of faeces removal rate (Table 1). There was a significant two-way interaction term between parental sex and brood age (Table 1) owing to a significant decrease in male faeces removal rates on day 12 relative to day 8 (LSD a posteriori test, $P = 0.002$), and a significant increase in female faeces removal rates on day 12 relative to day 8 (LSD a posteriori test, $P = 0.012$).

PARENTAL BODY MASS

Controlling for the effect of tarsus length, repeated-measures ANCOVAs were performed to separate the effects of experimental group and brood age (days 8 and 12) on parental body mass changes. For males,

Table 2. Mean \pm SD male and female mass (g) on days 9 and 15 after hatching of their brood with respect to experimental treatment. Sample sizes in parentheses

	Male handicapped	Control	Female handicapped
Male mass on day 9	18.06 \pm 0.75 (27)	18.09 \pm 0.80 (29)	18.32 \pm 0.71 (26)
Male mass on day 15	17.80 \pm 0.66 (21)	17.95 \pm 0.83 (26)	18.11 \pm 0.73 (24)
Female mass on day 9	17.31 \pm 0.59 (27)	17.24 \pm 0.83 (33)	17.47 \pm 0.74 (30)
Female mass on day 15	17.28 \pm 0.81 (25)	16.93 \pm 0.68 (28)	16.87 \pm 0.70 (28)

body mass did not differ among experimental group (repeated-measures ANCOVA; $F_{2,64} = 0.74$, $P = 0.48$), but significantly differed between days 8 and 12 ($F_{1,64} = 9.99$, $P = 0.002$; Table 2), with lower values on day 12 (LSD a posteriori test, $P = 0.002$). Moreover, there was no significant experimental group by brood age interaction effect ($F_{2,64} = 0.45$, $P = 0.64$). Also for females, body mass did not differ among experimental groups, although the effect was close to significant ($F_{2,77} = 2.75$, $P = 0.07$; Table 2), and significantly differed between days 8 and 12 ($F_{1,77} = 14.05$, $P < 0.001$), with lower values on day 12 (LSD a posteriori test, $P < 0.001$). There was, however, a significant two-way interaction term between experimental group and brood age ($F_{2,77} = 4.28$, $P = 0.017$) owing to a non-significant change in female body mass between days 8 and 12 by both control and females with a handicapped partner (LSD a posteriori tests, $P = 0.10$ and $P = 0.68$, respectively), and to a significant decrease by handicapped females (LSD a posteriori test, $P < 0.001$; Table 2).

BROOD SURVIVAL AND GROWTH

There was no effect of experimental treatment on nestling survival from days 8–14 after hatching (Table 3). Nestling body mass on day 8 after hatching did not differ among experimental groups (Table 3). Mean nestling tarsus length on day 14 after hatching did not differ among experimental groups (Table 3). Also mean nestling body mass on day 14 after hatching did not differ among experimental groups, although the effect was close to significant with lower values for the handicapped groups (Table 3). As nestling mass on day 14 may depend on initial mass, an ANCOVA was performed with experimental treatment as factor and nestling mass on day 8 as covariate. There was no significant experimental treatment effect on nestling mass on day 14 after hatching when controlling for the effect

of initial nestling body mass (ANCOVA; experimental treatment: $F_{2,85} = 2.60$, $P = 0.08$; nestling mass on day 8: $F_{1,85} = 57.35$, $P < 0.001$). Furthermore, the increase in nestling body mass from days 8 to 14 after hatching did not differ among experimental groups (Table 3).

Discussion

We showed that in great tits the sexes reacted differentially to being handicapped. In handicapped males feeding rates decreased, while in handicapped females condition deteriorated. Females with a handicapped partner fully compensated for their partner's decrease in feeding rate, while males with a handicapped partner tended to do less. The effects of handicapping one partner on the offspring were non-significant.

Since handicapping decreases the wing area, it increases the wing loading and thus costs of flight (Pennycuik 1982). Therefore, handicapped birds might be expected to decrease their faeces removal rate to reduce their wing loading. However, there was no effect of experimental treatment on the faeces removal rate from both parents. The extra amount of energy needed to remove a faecal sac from the nestbox is probably small compared to a feeding visit without removing a faeces sac, due to the short distance great tits fly with the faeces in their bill.

The amount of food that parents delivered to the nest depends not only on the feeding rate, but also on what is delivered (Whittingham *et al.* 1994). Previous studies show that parents may be able to maintain the frequency of their feeding visits by switching to prey types that were more quickly gathered (Tinbergen 1981; Lifjeld 1988; Wright & Cuthill 1989; 1990a,b) or to smaller prey types (Lifjeld 1988; Wright & Cuthill 1989, 1990a,b). Therefore, an increase in the feeding rate does not necessarily mean an increase in food delivery.

Table 3. Nestling survival (mean \pm SD, %) from day 8 to day 14 after hatching, nestling mass (g) on days 8 and 14 after hatching, tarsus length (mm) and the increase in nestling body mass from days 8–14 after hatching in the three experimental groups. Sample sizes are in parentheses

	Male handicapped	Control	Female handicapped	<i>F</i>	<i>P</i>
Nestling survival	98.55 \pm 4.28 (27)	97.28 \pm 8.07 (33)	98.45 \pm 5.00 (30)	0.18	0.83
Nestling mass (8-day-old)	12.66 \pm 1.64 (26)	12.96 \pm 1.78 (33)	12.53 \pm 1.53 (30)	0.55	0.58
Nestling mass (14-day-old)	16.19 \pm 1.50 (27)	17.05 \pm 1.00 (33)	16.42 \pm 1.65 (30)	3.03	0.052
Nestling tarsus (14-day-old)	19.25 \pm 0.70 (27)	19.56 \pm 0.58 (33)	19.46 \pm 0.62 (30)	1.78	0.17
Nestling mass change (days 8–14)	3.66 \pm 1.24 (26)	4.13 \pm 1.39 (33)	3.94 \pm 1.33 (30)	0.95	0.39

Nestling survival and body mass development is in this respect our best estimate of food delivery to the nest, but can not be quantified for each partner separately. There was no effect of experimental treatment on nestling survival from day 8–14 after hatching. Nestling body mass on day 14 after hatching tended to be lower in both groups with a handicapped parent, suggesting that their partners did not compensate completely. However, since this difference was insignificant and since total feedings per nest were not statistically different, we assume for this discussion that the amount of food delivered per visit was not affected by handicapping.

The fact that the sexes did respond differentially to handicapping is a fascinating finding. The magnitude of response ought to depend on the relative costs and benefits of increasing parental effort (Winkler 1987). Adult mass losses during the nestling period have been interpreted as adaptive, for instance due to a reduced cost of flight when this activity becomes increasingly important (Freed 1981; Norberg 1981; Ricklefs & Hussell 1984), but fitness costs and benefits as functions of body mass are poorly understood. The fact that males and females responded differentially suggests that costs and/or benefits of mass change and feeding effort differ between sexes. Although the share of the sexes in feeding is roughly equal in the great tit half-way through the nestling period (Smith *et al.* 1988) the tasks of male and female do differ in the early nestling phase, where females brood the young (Verhulst 1995), and perhaps more relevant, after fledging. Particularly when the pair starts a second clutch, the share of the male in feeding offspring is larger than that of the female (Verhulst & Hut 1996). One line of thought is that there is a trade-off for both sexes between feeding rate and body mass. Males have to defend the territory (Kluyver 1951) and a high body mass might be more beneficial for them in that respect. The fitness cost of being lighter may therefore be higher for the males resulting in a relative stable body mass, but a decline in feeding rate after handicapping relative of the female. Alternatively, feeding offspring is more costly or less beneficial to the male than to the female resulting in the same response. For this latter scenario Slagsvold & Lifjeld (1990) suggested that the male's lack of confidence in paternity may cause him to value the benefits of feeding lower than the female. Further research on this question should attempt to quantify fitness effects of body mass and feeding rate for the sexes independently.

Females in the male handicapped group compensated to an equivalent degree for their partner's lower parental care. A compensatory response protects the young from the detrimental effects of reduction in the amount of food delivered to the nest. On the other hand, the non-compensation by

males in the female handicapped group have been the result of them being unable to respond to the shortfall in their partner's work rate, either because of some physical time limit upon rate at which food could be collected (Wright & Cuthill 1990b), because they worked at some physiological maximum (Drent & Daan 1980) or because they were unwilling to pay the costs in terms of future survival. However, the reason why females great tits seemed to invest more heavily than males, when necessary, is unknown (Slagsvold & Lifjeld 1990).

Theoretical models suggest that an equality of female and male investment is evolutionarily stable in bi-parental species (Chase 1980; Houston & Davies 1985). The response of a parent to a reduction in parental care by its partner has been investigated by handicapping the partner to cause a reduction in its parental effort. Published studies are likely to be biased in the reported effects of handicapping on care since the main goal of these manipulations was to reduce the level of care by one parent and see how its partners responded (Wright & Cuthill 1989). These studies were not interested in the response of the birds to handicapping, only that it reduced its provisioning rate. Table 4 summarizes the effects of handicapping one parent on feeding rates and parental condition of both parents. Although the experimental design varied widely, general trends can be derived from these experimental studies. Passerines show a significant decline in both their feeding rates and body condition as a response to being handicapped (Table 4). Some studies implicitly assumed that handicapping causes a reduction in parental care of the handicapped parents by using one-tailed statistical tests (Slagsvold & Lifjeld 1988, 1990). Although published studies including this study never showed an increase in provisioning rate by handicapping birds, an increase in parental care can theoretically also be an optimal response to being handicapped (type 2 effect; see Introduction).

To assess the type of effect handicapping may have on the survival-effort curve, the empirical data can be interpreted in terms of changes in the model variables. Under the assumptions described in the introduction and assuming the observed feeding rates to represent the optimal effort as a response to being handicapped, the observed values can be interpreted in terms of the parameters c and f . Regardless of their significance, the observed change in feeding rate can be expressed as a percentage of the feeding rate before handicapping (on day 8 after hatching of their brood). The default level of parental care in the model is 0.333 (see equations 6 and 7, where $f = c = 1$) and corresponding changes from the default level in the model were calculated (translated values; Table 5).

Table 4. Handicapping studies in which the effect on parental feeding rates and body condition was monitored

Species	Parent handicapped	Male feeding rate	Female feeding rate	Total feeding rate	Male condition	Female condition	Reference
<i>Thalassoica antarctica</i>	(1)	Decrease*	No change	Decrease*	No change	No change	Sæther <i>et al.</i> (1993)
<i>Pachyptila belcheri</i>	(4)	(2)	(3)	No change	Decrease*	(3)	Weimerskirch <i>et al.</i> (1995)
<i>Larus argentatus</i>	(1)	No change	No change	No change			Verbeek & Morgan (1980)
<i>Tachycineta bicolor</i>	Male	Decrease*	Increase	No change			Whittingham <i>et al.</i> (1994)
<i>Ficedula hypoleuca</i>	Female	No change	Decrease*	Decrease*		Decrease*	Slagsvold & Lifjeld (1988)
<i>Parus caeruleus</i>	Female	No change	Decrease*	Decrease*		Decrease*	Slagsvold & Lifjeld (1990)
<i>Parus ater</i>	Male	Decrease*	No change	Decrease*	No change		
	Female					Decrease*	Slagsvold & Lifjeld (1990)
<i>Parus major</i>	Male	Decrease*	Decrease	Decrease	No change		
	Female					Decrease*	Slagsvold & Lifjeld (1990)
<i>Parus major</i>	Female	No change	Decrease	No change	No change	Decrease*	Present study
	Male	Decrease*	Increase*	No change	No change	No change	
<i>Sturnus vulgaris</i>	Female	Increase*	Decrease*	Decrease*			Wright & Cuthill (1989)
	Male	Decrease*	Increase*	Decrease*			
<i>Sturnus vulgaris</i>	Female	Increase*	Decrease	Increase			Wright & Cuthill (1990a)
	Male	Decrease	Increase*	Increase			
<i>Sturnus vulgaris</i>	Female	Increase*	Decrease*	No change			Wright & Cuthill (1990b)
	Male	Decrease*	Increase*	No change			
<i>Nectarinia osea</i>	Female	Increase*	Decrease*	Decrease*			Markman <i>et al.</i> (1995)

(1) No distinction was made between female and male.

(2) Sex unknown: handicapped parent.

(3) Sex unknown: non-handicapped parent.

(4) Both member of the pair were handicapped.

* Significantly different from the control.

Although it is often suggested that a reduction in body mass is accompanied by a lower survival probability (Drent & Daan 1980; Drent 1984; Nur 1984), it proves to be extremely difficult to quantitatively relate body mass losses and survival. Therefore, the decline in body mass of handicapped females was interpreted in terms of decreased survival probability at three different levels (1, 5 and 10%; Table 5). The survival probability of males (as estimated by body mass change) is assumed not to be influenced by handicapping since the change in body mass of handicapped males approximates the change in body mass of control males (Table 2). The default

survival level in our model for both sexes was taken as 0.487 (see equation 1, where $f = c = 1$).

Having interpreted our empirical results on condition and effort in terms of deviations from the default level in our model, we calculated the c - f combination (*i.e.* survival-effort curve) that would predict the observed response as being optimal. With equations 2 and 6 we had two equations in which two of the four parameters were known (survival and effort) and thus the remaining 2 (c and f) could be calculated. For males, there is only one specific effect of handicapping on the survival-effort curve, in which both translated effort and survival probability can be regarded as an optimal response

Table 5. Empirical changes in effort and survival due to handicapping (where the decline in female condition has been interpreted in a decline in survival probability of 1, 5 and 10%), the default level of both variables in the model and the translation of empirical changes in model variables. Parameters c and f calculated were based on the translated values

Handicapped sex	Variable	Empirical (%)	Default	Translated	Parameter c	Parameter f
Male	Effort	-39.20	0.333	0.202		
	Survival	0	0.487	0.487	1.251	0.925
Female	Effort	-25.54	0.333	0.255		
	Survival	1	0.487	0.482	1.142	0.949
	Survival	5	0.487	0.463	1.171	0.919
	Survival	10	0.487	0.438	1.213	0.878

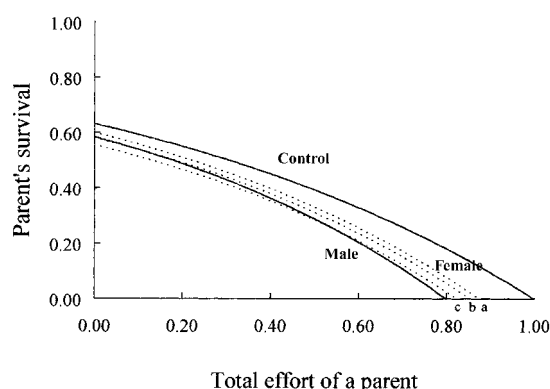


Fig. 4. Relationship between parental effort and survival for both males and females, based on the results of the present study. The three curves of female survival represent the levels on which the decline in female body mass might act on survival ($a = 1\%$, $b = 5\%$ or $c = 10\%$ decreased survival probability).

(Table 5). For females, the effect of handicapping on the survival–effort curve depends on the relationship between body mass losses and survival, and three pairs of c – f combinations were calculated for handicapped females (Table 5). The effect of handicapping on the survival–effort curves for both males and females appears to be a type 3 effect (see Introduction). However, the handicapped male's survival–effort curve appeared to be slightly steeper than that of handicapped females (Fig. 4). It can be seen in Fig. 4 that males suffer more from an increase in effort (type 1 effect), whereas females are relatively more affected through other variables than feeding efficiency (e.g. predator avoidance, type 2 effect).

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